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Gene Frequency and Genetic Variability of a Metric Character[1]

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Abstract : This paper studies the magnitudes of the additive variance, genetic variance and the heritability in relation to the gene frequency for different degrees of dominance. The gene frequencies yielding the maximum values of additive variance, genetic variance and the heritability are also determined over a wide range of dominance. Several sizes of environmental variation have been taken into account to reflect the real-world situation. Results indicated that selection for maximizing the genetic variance or additive variance does not result in maximizing the genetic gain. It should be selected for maximizing the heritability in order to achieve the largest population improvement. A single-locus with two-allele system is considered only for the purpose of deduction, but the results derived could reprsent the average effect of a multi-loci system. The effects of epistasis, linkage, and genotype-environment interaction on the genetic variability of a metric character are briefly discussed.

INTRODUCTION

Gene freguency plays a major role in the study of quantitative inheritance of a metric character, which in turn is the foundation of genetic selection for population improvement. Gene frequency is stable in a large random-mating population in the absence of agencies tending to change its genetic properties, and selection is the most effective way in changing the gene frequency, and thus the mean and variance, in a population for the purpose of genetic improvement. Gene frequency determines the size of components of genetic variation of a metric character. It is the relative magnitude of these variation components that the genetic properties of the population are determined. Therefore, population improvement by selection is in fact changing the gene frequencies of that population.

This paper studies the magnitudes of the additive variance, genetic variance and the heritability in relation to the gene frequency for different degrees of dominance. Gene frequencies yielding the maximum values of additive variance, genetic variance and the heritability are also determined over a wide range of dominance. Several sizes of the environmental variance have been taken into account to reflect the real-world

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situation.

Throughout this paper, only a single-locus with two-allele system has been considered for the purpose of explanation and deduction. Nevertheless, the results derived could also represent the average effect of a multi-loci system [5]. Complexity arising from the dependence of genes in action (epistasis), dependence of genes in inheritance (linkage) and the genotype-environment interaction are briefly discussed.

GENE FREQUENCY AND GENETIC VARIABILITY

The genetic properties of a population may be expressed in terms of the gene frequencies and genotype frequencies. However, the concept of 'value,' expressed in the metric units, is needed in order to deduce the connection between the gene frequencies and the quantitative differences exhibited in a metric character.

The value observed when the character is measured on an individual is the phenotypic value of that individual. In order to analyze the genetic properties of the population we have to divide the phenotypic value into components attributable to different causes. The phenotypic value is first divided into components attributable to the influence of genotype and environment. Without lose of generality, we could assign arbitrary values to the genotypes for the purpose of deduction.

Following Falconer [2], values of genotypes in a two-allele system, measured as deviations from the population mean, are shown in Table 1. The average effect of a gene is the mean deviation from the population mean of individuals which received that gene from one parent, the gene received from the other parent having come at random from the population (Table 1). The genotypic values are again divided into the breeding values and the dominance deviations. The breeding value is also referred to as the 'additive genotype', and variation in breeding value called the 'additive effects' of genes. The dominance deviation arises from the property of dominance among the alleles at a locus.

As the phenotypic value can be divided into seperate components, so does the variance of phenotypic values. The components of variance and the values whose variance they measure can also be found in the last column of Table 1.

Table 1. Values of genotypes, measured as deviations from the population mean, and the variance components measuring their variances in a two-allele system.

	Genotype			Variance component
	YY	Yy	yy	
Frequency	p^2	$2pq$	q^2	—
Assigned value	a	d	$-a$	—
Genotypic value	$2q(s-qd)$	$(q-p)s+2pqd$	$-2p(s+pd)$	$Vg=2pqs^2+(2pqd)^2$
Breeding value	$2qs$	$(q-p)s$	$-2ps$	$Va=2pqs^2$
Dominance deviation	$-2q^2d$	$2pqd$	$-2p^2d$	$Vd=(2pqd)^2$
Environmental deviation	e_1	e_2	e_3	Ve
Phenotypic value	$2q(s-qd)+e_1$	$(q-p)s+2pqd+e_2$	$-2p(s+pd)+e_3$	$Vp=Vg+Ve=Va+Vd+Ve$

Environmental deviation mean : $E=0$.
Population mean : $M=a(p-q)+2dpq$.
Average effect of gene-subsititution : $s=a+d(q-p)$.

The heritability of a metric character expresses the proportion of the total variance that is attributable to the average effects of genes, and this is what determines the degree of resemblance between relatives. The most important function of the heritability in the genetic study of metric characters is its predictive role. We can only measure the phenotypic values of individuals, but it is the breeding value that determines their influence on the next generation. The heritability expresses the degree of reliability of the phenotypic value as a guide to the breeding value. The heritability is defined as the ratio of additive variance to phenotypic variance : $h^2=Va/Vp$.

In the following text the term 'gene frequency' is referred to p (see Table 1) unless otherwise specified.

1. Gene frequency yielding maximum additive variance

Since

$$Va=2pq[a+d(q-p)]^2,$$

gene frequency yielding the maximum value of additive variance may be found by partially differentiating the additive variance with respect to p (gene freguency). It is not difficult to verify that

$$p=1-[(a+4d)-\sqrt{(a^2+8d^2)}]/8d \quad \text{for } d<0,$$
$$=0.5 \quad \text{for } d=0,$$
$$=[(a+4d)-\sqrt{(a^2+8d^2)}]/8d \quad \text{for } d>0,$$

yields the maximum value of additive variance.

Gene frequencies yielding the maximum additive variances for different degrees of dominance are shown in Table 2 along with the heritabilities under various magnitudes of the environmental variance.

It can be seen that gene frequency resulting in maximum additive variance is determined by the degree of dominance (Table 2). The distribution of the additive variance in relation to the gene frequency is symmetrical when there is no dominance. But the distribution is positively skewed when there is positive dominance and negatively skewed when there is negative dominance. The maximum additive variance attainable increases along with the increase of the dominance. At the gene fregency yielding the maximum additive variance, the heritability decreases as the environmental variance increases for any given degree of dominance. When there is environmental variation present, the heritability gradually increases as the degree of dominance increases. It is noted that when there is no environmental variation, the heritability decreases as the degree of dominance increases. This is because that the gene frequency yielding maximum additive variance also increases the genetic variance and the rate of increase of the latter is faster than that of the former (Table 2).

Table 2. Gene frequency yielding maximum additive variance for different degrees of dominance (d). Heritab'lities under various magnituedes of environmental variance (Ve) are also shown. Gene frequency designates p for positive dominance and designates q for negative dominacne.

a	| d |	Gene freq.	Additive variance	Genetic variance	Heritability				
					Ve=0	Ve=50	Ve=100	Ve=200	Ve=300
10	0	0.500	50.000	50.000	1.000	0.500	0.333	0.200	0.143
10	1	0.451	50.495	50.740	0.995	0.501	0.335	0.201	0.144
10	2	0.407	51.928	52.860	0.982	0.505	0.340	0.205	0.147
10	3	0.370	54.176	56.133	0.965	0.510	0.347	0.212	0.152
10	4	0.341	57.105	60.333	0.946	0.518	0.356	0.219	0.158
10	5	0.317	60.601	65.288	0.928	0.526	0.367	0.228	0.166
10	6	0.298	64.581	70.882	0.911	0.534	0.378	0.238	0.174
10	7	0.282	68.986	77.038	0.895	0.543	0.390	0.249	0.183
10	8	0.270	73.772	83.703	0.881	0.552	0.402	0.260	0.192
10	9	0.259	78.909	90.845	0.869	0.560	0.413	0.271	0.202
10	10	0.250	84.375	98.438	0.857	0.568	0.425	0.283	0.212
10	11	0.242	90.154	106.465	0.847	0.576	0.437	0.294	0.222
10	12	0.236	96.234	114.914	0.837	0.584	0.448	0.306	0.232
10	13	0.230	102.605	123.776	0.829	0.590	0.459	0.317	0.242
10	14	0.225	109.260	133.044	0.821	0.597	0.469	0.328	0.252
10	15	0.220	116.194	142.712	0.814	0.603	0.479	0.339	0.262
10	16	0.216	123.402	152.776	0.808	0.609	0.488	0.350	0.273
10	17	0.212	130.880	163.232	0.802	0.614	0.497	0.360	0.283
10	18	0.209	138.626	174.079	0.796	0.619	0.506	0.371	0.292
10	19	0.206	146.636	185.314	0.791	0.623	0.514	0.381	0.302
10	20	0.203	154.910	196.935	0.787	0.627	0.522	0.390	0.312
10	21	0.201	163.446	208.941	0.782	0.631	0.529	0.400	0.321
10	22	0.199	172.242	221.331	0.778	0.635	0.536	0.409	0.330
10	23	0.197	181.296	234.102	0.774	0.638	0.543	0.418	0.339
10	24	0.195	190.609	247.256	0.771	0.641	0.549	0.426	0.348
10	25	0.193	200.178	260.790	0.768	0.644	0.555	0.434	0.357

2. Gene frequency yielding maximum guentic variance

Since

$$Vg=2pq[a+d(q-p)]^2+(2pqd)^2,$$

as we did for additive variance, gene frequency yielding the maximum value of genetic variance is found by taking the partial differentiation of the genetic variance with respect to p. After a little algebraic simplification and deduction, the solution is found to be:

a. $p=a[(1+d/a)/2+\sqrt{(2/3)}\cdot\cos(\theta+2\pi/3)]/d$

for $d>0$ and $d\leq\sqrt{[1+\sqrt{(32/27}\,]}\cdot a$,

where $\theta=\cos^{-1}[\sqrt{(27/32)}\cdot(1-d^2/a^2)]/3$.

b. $p=a[(1+d/a)/2-\sqrt{(2/3)}\cdot\cos\theta]/d$

for $d<0$ and $d\geqq-\sqrt{[1+\sqrt{(32/27)}]}\cdot a$,

where $\theta=\cos^{-1}[\sqrt{(27/32)}\cdot(d^2/a^2-1)]/3$.

c. $p=(a+d)/2d+a[\sqrt[3]{(C+D)}+\sqrt[3]{(C-D)}]/d$

for $d\neq0$ and $|d|>\sqrt{[1+\sqrt{(32/27)}]}\cdot a$,

where $C=(1-d^2/a^2)/16$ and $D=\sqrt{(C^2-1/216)}$.

d. $p=0.5$ for $d=0$

Gene frequencies which have the maximum genetic variances for different degrees of dominance are given in Table 3 along with the heritabilities under various magnitudes of the environmental variance.

Table 3. Gene frequency yielding maximum genetic variance for different degrees of dominance (d). Heritabilities under various magnituedes of environmental variance (Ve) are also shown. Gene frequency designates p for positive dominance and designates q for negative dominance.

a	| d |	Gene freq	Additive variance	Genetic variance	Hreitability				
					Ve=0	Ve=50	Ve=100	Ve=200	Ve=300
10	0	0.500	50.000	50.000	1.000	0.500	0.333	0.200	0.143
10	1	0.451	50.495	50.740	0.995	0.501	0.335	0.201	0.144
10	2	0.410	51.926	52.862	0.982	0.505	0.340	0.205	0.147
10	3	0.378	54.161	56.149	0.965	0.510	0.347	0.211	0.152
10	4	0.354	57.049	60.392	0.945	0.517	0.356	0.219	0.158
10	5	0.336	60.463	65.434	0.924	0.524	0.365	0.228	0.165
10	6	0.322	64.307	71.172	0.904	0.531	0.376	0.237	0.173
10	7	0.312	68.510	77.535	0.884	0.537	0.386	0.247	0.181
10	8	0.304	73.024	84.480	0.864	0.543	0.396	0.257	0.190
10	9	0.298	77.811	91.975	0.846	0.548	0.405	0.266	0.199
10	10	0.293	82.843	100.000	0.828	0.552	0.414	0.276	0.207
10	11	0.289	88.099	108.540	0.812	0.556	0.422	0.286	0.216
10	12	0.286	93.562	117.584	0.796	0.558	0.430	0.295	0.224
10	13	0.284	99.219	127.127	0.780	0.560	0.437	0.303	0.232
10	14	0.282	105.058	137.161	0.766	0.561	0.443	0.312	0.240
10	15	0.280	111.069	147.684	0.752	0.562	0.448	0.319	0.248
10	16	0.279	117.246	158.693	0.739	0.562	0.453	0.327	0.256
10	17	0.278	123.580	170.186	0.726	0.561	0.457	0.334	0.263
10	18	0.277	130.067	182.161	0.714	0.560	0.461	0.340	0.270
10	19	0.277	136.699	194.617	0.702	0.559	0.464	0.346	0.276
10	20	0.277	143.473	207.554	0.691	0.557	0.466	0.352	0.283
10	21	0.276	150.384	220.972	0.681	0.555	0.469	0.357	0.289
10	22	0.276	157.428	234.870	0.670	0.553	0.470	0.362	0.294
10	23	0.276	164.601	249.247	0.660	0.550	0.471	0.366	0.300
10	24	0.277	171.900	264.105	0.651	0.547	0.472	0.370	0.305
10	25	0.277	179.321	279.443	0.642	0.544	0.473	0.374	0.309

Gene frequency resulting in maximum genetic variance is also determined by the degree of dominance (Table 3) and is higher than that yielding the maximum additive variance. The distribution of the genetic variance in relation to gene freguency is, like that of additive variance, symmetrical for no dominance, positively skewed for positive dominance and negatively skewed for negative dominance. At the gene frequency yielding the maximum genetic variance, the heritability decreases as the environmental variance increases. The heritability usually increases as the degree of dominance increases, but the increasing speed under large environmental variance is higher than that under small environmental variance. When there is no environmental variance, the heritability decreases as the dominance increases, as we have seen in discussing the maximum additive variance in relation to the gene frequency. This is because the increasing rate of genetic variance is higher than that of the additive variance as the dominance increases (Table 3).

3. Gene frequency yielding maximum heritability

Heritability is expressed as

$$h^2 = Va/Vp$$
$$= 2pqs^2/(2pqs^2+4p^2q^2d^2+Ve)$$
where $s=a+d(q-p)$.

Again, we partially differentiate it with respect to p to get the gene frequency which maximize (or minimize) the heritability. After simplification, the answer is found to be the relavent solution of the following equation :

$$8ad^2p^5-4d^2(5a+d)p^4+8d^2(2a+d)p^3-4d(ad+d^2-2Ve)p^2$$
$$-2(a+4d)Vep+(a+d)Ve=0 \cdots\cdots (1)$$

When there is no environmental variation (Ve=0), the solution to Equation 1 has the minimum value of heritability and the maximum value is always 1. Gene frequencies yielding the minimum heritabilities for different degrees of dominance under no environmental variation are listed in Table 4.

Table 4. Gene frequency yieiding minimum heritability for different degrees of dominance (d) under no environmental variance. Maximum heritability is always 1. Gene frequency designates p for positive dominance and designates q for negative dominance.

a	| d |	Gene frequency	Additive variance	Genetic variance	Heritability
10	0	—	—	—	—
10	1	0.5500	48.5150	48.7600	0.9950
10	2	0.6000	44.2368	45.1584	0.9796
10	3	0.6500	37.6786	39.5418	0.9529
10	4	0.7000	29.6352	32.4576	0.9130
10	5	0.7500	21.0938	24.6094	0.8571
10	6	0.8000	13.1072	16.7936	0.7805
10	7	0.8500	6.6326	9.8188	0.6755
10	8	0.9000	2.3328	4.4064	0.5294
10	9	0.9500	0.3430	1.0740	0.3193
10	10	1.0000	0.0000	0.0000	0.0000
10	11	0.9545	0.0000	0.9112	0.0000
10	12	0.9167	0.0000	3.3611	0.0000
10	13	0.8846	0.0000	7.0429	0.0000
10	14	0.8571	0.0000	11.7551	0.0000
10	15	0.8333	0.0000	17.3611	0.0000
10	16	0.8125	0.0000	23.7656	0.0000
10	17	0.7941	0.0000	30.9005	0.0000
10	18	0.7778	0.0000	38.7160	0.0000
10	19	0.7632	0.0000	47.1752	0.0000
10	20	0.7500	0.0000	56.2500	0.0000
10	21	0.7381	0.0000	65.9189	0.0000
10	22	0.7273	0.0000	76.1653	0.0000
10	23	0.7174	0.0000	86.9759	0.0000
10	24	0.7083	0.0000	98.3403	0.0000
10	25	0.7000	0.0000	110.2500	0.0000

On the contrary to zero environmental variation, the solution to Equation 1 gives the maximum value of heritability when there is environmental variation present. Gene frequencies yielding the maximum heritabilities for different degrees of dominance under various magnitudes of environmental variation are given in Table 5 to Table 8.

Table 5. Gene frequency yieiding minimum heritability for different degrees of dominance (d) under 50-unit of environmental variance. Minimum heritability is always 0. Gene frequency designates p for positive dominance and designates q for negative dominance.

a	| d |	Gene frequency	Additive variance	Genetic variance	Heritability
10	0	0.5000	50.0000	50.0000	0.5000
10	1	0.4505	50.4951	50.7402	0.5012
10	2	0.4038	51.9259	52.8532	0.5049
10	3	0.3618	54.1564	56.0759	0.5105
10	4	0.3256	57.0261	60.1117	0.5179
10	5	0.2948	60.3939	64.7164	0.5265
10	6	0.2690	64.1522	69.7195	0.5359
10	7	0.2472	68.2236	75.0100	0.5457
10	8	0.2287	72.5526	80.5165	0.5559
10	9	0.2128	77.0985	86.1919	0.5661
10	10	0.1991	81.8303	92.0038	0.5763
10	11	0.1872	86.7243	97.9288	0.5863
10	12	0.1767	91.7612	103.9497	0.5960
10	13	0.1674	96.9254	110.0531	0.6056
10	14	0.1590	102.2039	116.2283	0.6148
10	15	0.1516	107.5856	122.4668	0.6238
10	16	0.1448	113.0611	128.7613	0.6325
10	17	0.1386	118.6222	135.1060	0.6408
10	18	0.1330	124.2616	141.4958	0.4689
10	19	0.1278	129.9733	147.9263	0.6567
10	20	0.1231	135.7514	154.3937	0.6642
10	21	0.1187	141.5911	160.8947	0.6714
10	22	0.1146	147.4880	167.4265	0.6783
10	23	0.1108	153.4379	173.9865	0.6850
10	24	0.1073	159.4372	180.5725	0.6915
10	25	0.1040	165.4828	187.1825	0.6977

Table 6. Gene frequency yieiding minimum heritability for different degrees of dominance (d) under 100-unit of environmental variance. Minimum heritability is always 0. Gene frequency desinagtes p for positive dominance and designates q for negative dominance.

a	| d |	Gene frequency	Additive variance	Genetic variance	Heritability
10	0	0.5000	50.0000	50.0000	0.3333
10	1	0.4507	50.4951	50.7403	0.3350
10	2	0.4054	51.9277	52.8573	0.3397
10	3	0.3660	54.1714	56.1099	0.3470
10	4	0.3330	57.0848	60.2424	0.3562
10	5	0.3056	60.5468	65.0498	0.3668
10	6	0.2827	64.4646	70.3858	0.3783
10	7	0.2634	68.7692	76.1483	0.3904
10	8	0.2470	73.4093	82.2650	0.4028
10	9	0.2328	78.3458	88.6831	0.4152
10	10	0.2205	83.5480	95.3623	0.4277
10	11	0.2096	88.9913	102.2712	0.4400
10	12	0.1998	94.6551	109.3841	0.4521
10	13	0.1911	100.5221	116.6798	0.4639
10	14	0.1833	106.5772	124.1404	0.4755
10	15	0.1761	112.8072	131.7506	0.4868
10	16	0.1695	119.2005	139.4969	0.4977
10	17	0.1635	125.7465	147.3677	0.5083
10	18	0.1579	132.4356	155.3527	0.5186
10	19	0.1527	139.2592	163.4427	0.5286
10	20	0.1479	146.2093	171.6296	0.5383
10	21	0.1434	153.2786	179.9060	0.5476
10	22	0.1392	160.4604	188.2653	0.5566
10	23	0.1353	167.7485	196.7017	0.5654
10	24	0.1316	175.1370	205.2097	0.5738
10	25	0.1280	182.6206	213.7845	0.5820

Table 7. Geny frequency yieiding maximum heritability for different degrees of dominance (d) under 200-unit of environmental variance. Minimum heritability is always 0. Gene frequency designates p for positive dominance and designates q for negative dominance.

a	| d |	Gene frequency	Additive variance	Genetic variance	Heritability
10	0	0.5000	50.0000	50.0000	0.2000
10	1	0.4508	50.4951	50.7403	0.2014
10	2	0.4061	51.9282	52.8589	0.2054
10	3	0.3681	54.1751	56.1230	0.2115
10	4	0.3368	57.0997	60.2929	0.2194
10	5	0.3112	60.5871	65.1820	0.2285
10	6	0.2901	64.5509	70.6590	0.2385
10	7	0.2726	68.9279	76.6335	0.2492
10	8	0.2577	73.6726	83.0417	0.2603
10	9	0.2450	78.7506	89.8368	0.2717
10	10	0.2339	84.1362	96.9831	0.2833
10	11	0.2242	89.8088	104.4521	0.2950
10	12	0.2155	95.7517	112.2200	0.3067
10	13	0.2078	101.9508	120.2666	0.3183
10	14	0.2007	108.3941	128.5741	0.3299
10	15	0.1943	115.0708	137.1269	0.3413
10	16	0.1884	121.9712	145.9105	0.3526
10	17	0.1829	129.0865	154.9118	0.3637
10	18	0.1779	136.4084	164.1188	0.3746
10	19	0.1731	143.9291	173.5203	0.3853
10	20	0.1687	151.6413	183.1058	0.3958
10	21	0.1645	159.5379	192.8658	0.4061
10	22	0.1606	167.6124	202.7909	0.4161
10	23	0.1569	175.8582	212.8729	0.4259
10	24	0.1533	184.2693	223.1036	0.4355
10	25	0.1500	192.8398	233.4755	0.4449

Table 8. Gene frequency yieiding maximum heritability for different degrees of dominance (d) under 300-unit of environmental variance. Minimum heritability is always 0. Gene frequency designates p for positive dominance and designates q for negative dominance.

a	| d |	Gene frequency	Additive variance	Genetic variance	Heritability
10	0	0.5000	50.0000	50.0000	0.1429
10	1	0.4509	50.4951	50.7403	0.1440
10	2	0.4064	51.9282	52.8594	0.1472
10	3	0.3688	54.1758	56.1267	0.1521
10	4	0.3381	57.1025	60.3075	0.1585
10	5	0.3131	60.5948	65.2205	0.1659
10	6	0.2927	64.5676	70.7394	0.1742
10	7	0.2758	68.9594	76.7783	0.1830
10	8	0.2616	73.7262	83.2773	0.1924
10	9	0.2495	78.8356	90.1933	0.2020
10	10	0.2390	84.2634	97.4935	0.2120
10	11	0.2298	89.9910	105.1525	0.2221
10	12	0.2217	96.0036	113.1490	0.2324
10	13	0.2144	102.2891	121.4651	0.2427
10	14	0.2078	108.8372	130.0853	0.2531
10	15	0.2018	115.6391	138.9954	0.2634
10	16	0.1963	122.6870	148.1826	0.2737
10	17	0.1913	129.9735	157.6350	0.2840
10	18	0.1866	137.4922	167.3417	0.2942
10	19	0.1822	145.2367	177.2920	0.3043
10	20	0.1781	153.2011	187.4762	0.3143
10	21	0.1742	161.3798	197.8848	0.3241
10	22	0.1705	169.7672	208.5088	0.3339
10	23	0.1671	178.3580	219.3398	0.3434
10	24	0.1638	187.1470	230.3695	0.3529
10	25	0.1607	196.1291	241.5900	0.3621

Magnitude of the heritability in relation to the gene frequency for different degrees of dominance under no environmental variance can be seen in Fig. 1. When there is no environmental variance, only the minimum heritability exists. The maximum heritability does not exist if the gene frequency is not fixed. Gene frequency yielding the minimum heritability is larger than 0.5 for positive partial dominance and is smaller than 0.5 for negative partial dominance (Table 4). Gene frequency resulting in minimum heritability gradually shifts to 0.5 from the right with the increase of positive overdominance and to 0.5 from the left with the increase of negative overdominance.

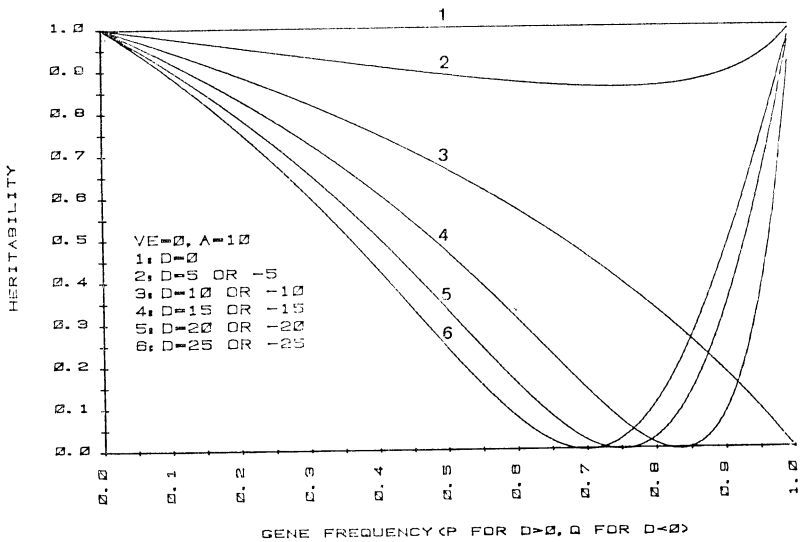

Fig. 1. Magnitude of heritability in relation to gene frequency for different degrees of dominance (D) under no environmental variance (VE).

When there is environmental variance present, and this is usually the case, the solution to Equation 1 gives the maximum heritability. Magnitude of the heritability in relation to the gene frequency for different degrees of dominance are plotted in Fig. 2 (for 50-unit of environmental variance), Fig. 3 (for 100-unit of environmental variance), Fig. 4 (for 200-unit of environmental variance)and Fig. 5 (for 300-unit of environmental variance).

From these figures, along with Table 5 to Table 8, we can see that for a given degree of environmental variance, the gene frequency that maximizes the heritability shifts from 0.5 to the left with the increase of positive dominance and shifts from 0.5 to the right with the increase of negative dominance. The maximum attainable heritability increases with the increase of dominance. It is interesting to note that when overdominance occurs, the distribution of heritability in relation to the gene frequency is a bi-modal one with higher peak on the left for positive overdominance and with higher peak on the right for negative overdominance.

For a given degree of dominance, gene frequencies resulting in maximum genetic variance (Table 3), maximum additive variance (Table 2) and maximum heritability

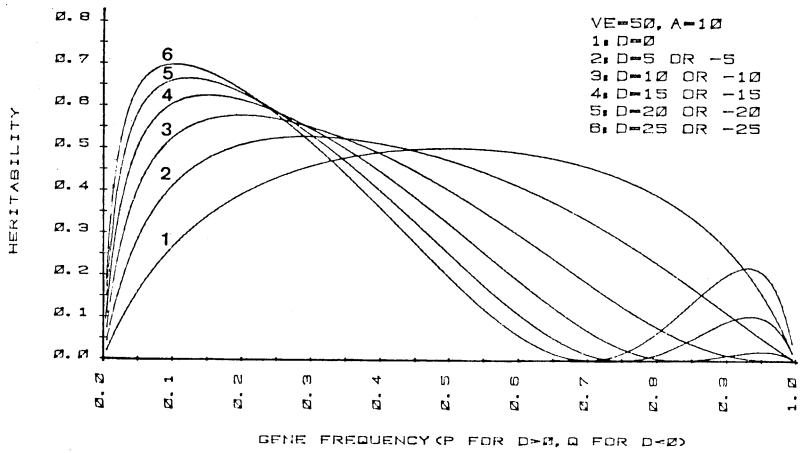

Fig. 2. Magnitude of heritability in relation to gene frequency for different degrees of dominance (D) under 50-unit of environmental variance (VE).

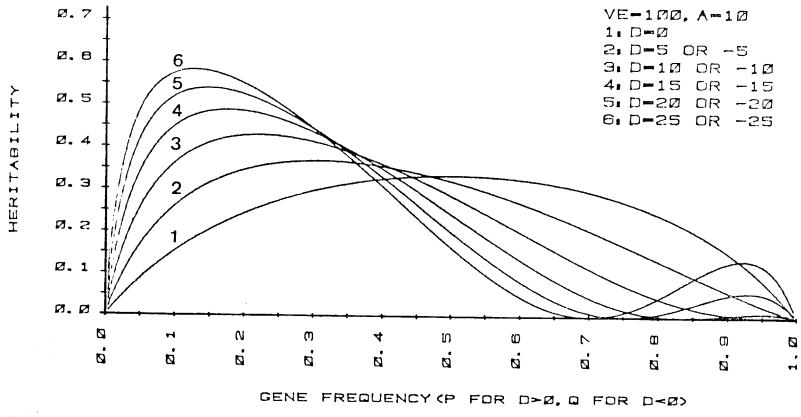

Fig. 3. Magnitude of heritability in relation to gene frequency for different degrees of dominance (D) under 100-unit of environmental variance (VE).

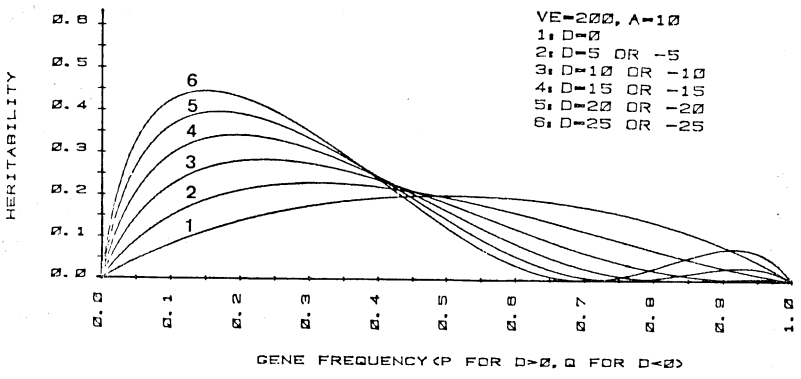

Fig. 4. Magnitude of heritability in relation to gene frequency for different degrees of dominance (D) under 200-unit of environmental variance (VE).

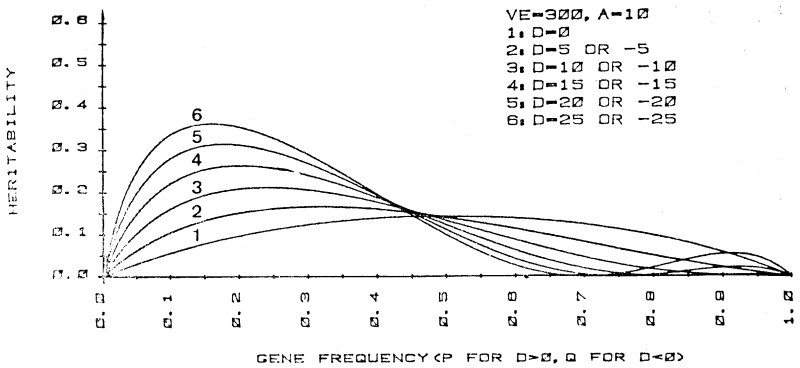

Fig. 5. Magnitude of heritability in relation to gene frequency for different degrees of dominance (D) under 300-unit of environmental variance (VE).

(Table 5 to Table 8) are in decreasing order for positive dominance and are in increasing order for negative dominance. This indicates that selection for maximizing the genetic variance or additive variance does not result in maximizing the genetic gain. It should be selected for maximizing the heritability in order to achieve the largest population improvement.

DISCUSSION

The contributions to the genetic variation of gene pairs at different loci are additive, in the way assumed in this paper, only if the genes at various loci are independent in both action and inheritance. Independence in action means that the increment added to a metric character in question by the substitution of one allele for another at a given locus is unaffected by the remaining genes under consideration. Dependence of genes in action means epistasis [5]. Throughtout this paper we confined our discussion to a single-locus with two-allele system. But the genetic variation of metric characters is in reality the product of segregation at some hundreds or thousands of loci. When only a single locus is considered the genotypic value is made up of the breeding value and the dominance deviation only. But when the genotype refers to more than one locus the genotypic value may include the epistatic deviation due to non-additive combination. In practice we can seperate the additive variance from the rest of the genetic variance, and so make the partition into additive, non-additive and environmental variance, $Vp=Va+(Vd+Vi)+Ve$, the dominance and interaction components being put together as non-additive variance. However, the amount of variance contributed by epistatic deviation is usually rather small and the neglect of it is therefore not likely to lead to serious error [2].

Independence of genes in inheritance means that the two alleles at one locus are equally likely to be transmitted from parent to offspring together with a given allele at the second locus. Dependence of genes in inheritance means linkage [5]. When the genes in question have no effects on viability, linkage does not affect the frequencies with which the alleles of each gene pairs are recovered in segregating generations [1]. Al-

though linkage does have its effect in partitioning the genetic variation, the effect of linkage on the value of a statistic could be zero even though linkage was in fact present; for the coupling and repulsion items, as well as the reinforcement and opposition items, could balance and thus cancel out[4,5]. The effect of linkage in partitioning the genetic variance will most probably render the dominance variance to include some of the interaction variance caused by linkage.

Another assumption we have made is that a specific difference of environments has the same effect on different genotypes. If this assumption is not justifiable, there is an interaction between genotypes and environments. An interaction between genotype and environment gives rise to an additional component of variance. This interaction variance can be isolated and measured by replicating genotypes under several different environments. Then an analysis of variance in a two-way classification of genotype×environment will yield estimates of the genotypic variance, the environmental variance and the genotype-environment interaction variance. In most cases the interactions are small relative to the genotypic and environmental effects and the interaction with heterozygotes genotypes is smaller than that with homozygotes in segregating generation[3,6]. Therefore, the variance due to genotype-environment interaction is best regarded as part of the environmental variation in the genetic study of a population unless differences of environments are under consideration, then the presence of genotype-environment interaction become important in connection with the specialization of breeds or varieties to local conditions.

A mathematical description of the complex genetic situation results in equations too cumbersome for solution. The Monte Carlo simulation by high-speed computer does not seem satisfactory either, due to too many subjectively assigned conditions. Although simple genetic model may lead to some departure from reality in the study of quantitative genetics, it is needed for the purpose of deduction. What we have previously discussed is the general effects of epistasis and linkage arising from a multi-loci system. and interaction between genotype and environment; detailed examination of these effects on the genetic variability of a me'ric character is to be made case by case.

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數量性狀之基因頻度與遺傳變異[1]

劉　清[2]

摘　要

本文探討在不同顯性程度下，基因頻度與累加性變方，遺傳變方及遺傳率之關係，導出形成最大累加性變方，遺傳變方及遺傳率之基因頻度值，並考慮不同程度之環境變異對其所產生的影響。結果顯示使遺傳變方或累加性變方爲最大之選拔並未能導致最大之遺傳獲得，只有使遺傳率爲最大之選拔方能造成最大之族羣改良。本文以一對基因之情況來描述基本遺傳系統並導出必要公式，所得推論亦可視爲多因子系統之一般結果。上位性作用，連鎖作用及遺傳一環境交感作用對一數量性狀遺傳變異之影響亦曾加討論。

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